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### **Incorporating metapopulation Dynamics to Inform Invasive Species Management: Evaluating Bighead and Silver Carp Control Strategies in the Illinois River**

Jahn Kallis

Richard Erickson

D. P. Coulter

Alison A. Coulter

Marybeth K. Brey

*See next page for additional authors*

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**Authors**

Jahn Kallis, Richard Erickson, D. P. Coulter, Alison A. Coulter, Marybeth K. Brey, Matt Catalano, John Dettmers, James Garvey, Kevin Irons, Elizabeth Marschall, Kenneth Rose, Mark Wildhaber, and David Glover

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## RESEARCH ARTICLE

# Incorporating metapopulation dynamics to inform invasive species management: Evaluating bighead and silver carp control strategies in the Illinois River

Jahn Kallis<sup>1</sup>  | Richard Erickson<sup>2</sup>  | David Coulter<sup>3,4</sup>  | Alison Coulter<sup>3</sup>  |  
Marybeth Brey<sup>2</sup>  | Matt Catalano<sup>5</sup> | John Dettmers<sup>6</sup>  | James Garvey<sup>4</sup>  |  
Kevin Irons<sup>7</sup> | Elizabeth Marschall<sup>8</sup>  | Kenneth Rose<sup>9</sup>  | Mark Wildhaber<sup>10</sup>  |  
David Glover<sup>11</sup> 

<sup>1</sup>U.S. Fish and Wildlife Service, Columbia Fish and Wildlife Conservation Office, Columbia, Missouri, USA; <sup>2</sup>U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, Wisconsin, USA; <sup>3</sup>Department of Natural Resource Management, South Dakota State University, Brookings, South Dakota, USA; <sup>4</sup>Center for Fisheries, Aquaculture, and Aquatic Sciences, Southern Illinois University, Carbondale, Illinois, USA; <sup>5</sup>School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, Auburn, Alabama, USA; <sup>6</sup>Great Lakes Fishery Commission, Ann Arbor, Michigan, USA; <sup>7</sup>Illinois Department of Natural Resources, Springfield, Illinois, USA; <sup>8</sup>Department of Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, Ohio, USA; <sup>9</sup>Center for Environmental Science, University of Maryland, Cambridge, Maryland, USA; <sup>10</sup>U.S. Geological Survey, Columbia Environmental Research Center, Columbia, Missouri, USA and <sup>11</sup>Illinois Department of Natural Resources, Havana, Illinois, USA

**Correspondence**

Jahn Kallis

Email: [jahn\\_kallis@fws.gov](mailto:jahn_kallis@fws.gov)**Funding information**

Great Lakes Restoration Initiative; USGS Biological Threats and Invasive Species Research Program

**Handling Editor:** Vitor Paiva**Abstract**

1. Invasive species management can benefit from predictive models that incorporate spatially explicit demographics and dispersal to guide resource allocation decisions.
2. We used invasive bigheaded carps (*Hypophthalmichthys* spp.) in the Illinois River, USA as a case study to create a spatially explicit model to evaluate the allocation of future management efforts. Specifically, we compared additional harvest (e.g. near the invasion front vs. source populations) and enhanced movement deterrents to meet the management goal of reducing abundance at the invasion front.
3. We found additional harvest in lower river pools (i.e. targeting source populations) more effectively limited population sizes upriver at the invasion front compared to allocating the same harvest levels near the invasion front. Likewise, decreasing passage (i.e. lock and dam structures) at the farthest, feasible downriver location limited invasion front population size more than placing movement deterrents farther upriver.
4. *Synthesis and applications.* Our work highlights the benefits of adopting a multi-pronged approach for invasive species management, combining suppression of source populations with disrupting movement between source and sink populations thereby producing compounding benefits for control. Our results also demonstrate the importance of considering metapopulation dynamics for invasive species control programs when achieving long-term management goals.

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**KEYWORDS**

aquatic invasive species, bighead carp, Illinois River, meta-populations, Mississippi River, population dynamics, silver carp, source-sink

## 1 | INTRODUCTION

Invasive species pose a threat to global biodiversity (Molnar et al., 2008). Management efforts to control invasive species require long-term policy decisions that are informed by the best available information (Epanchin-Niell & Wilen, 2012). Furthermore, these decisions need to be carefully developed, and ideally driven by empirical analyses (Love et al., 2018). Invasive species management actions can be expensive and time-intensive and determining effectiveness can take years leading to delays in adapting strategies (Love et al., 2018). Consequences of long-term policy decisions are high, as poor management of invasive species can have irreversible ecological, economic, and political outcomes crossing governmental boundaries.

Deciding how to deploy limited management resources to combat invasive species depends on the characteristics and dynamics of the species, ecosystem, and human stakeholders. Environmental heterogeneity within an invaded range can lead to spatial differences in species behaviour and population dynamics that must be considered when predicting the population responses of invasive species to potential management actions (Lustig et al., 2019). Accounting for metapopulation dynamics can be critical in managing advancing populations (Baker, 2017; Pepin et al., 2020). To this end, spatially explicit population models are an important tool for identifying and evaluating long-term management decisions (Day et al., 2018; Lustig et al., 2019). Models incorporating source-sink dynamics can be useful for understanding consequences of current management actions (Paquet et al., 2020), evaluating relative effects of management alternatives (e.g. removal versus movement deterrents; Pepin et al., 2020), and identifying critical locations to focus management actions (Baker, 2017; Pepin et al., 2020; Perry et al., 2017). The insights gained from these models can enhance the effectiveness of control programs despite the costs and challenges of collecting the spatially and temporally explicit data needed for the models.

Managing non-native, invasive carps has become an important conservation issue (Chapman et al., 2021). North American agencies have placed specific attention on controlling and containing silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*, collectively known as bigheaded carp. Managers particularly seek to prevent populations in the Mississippi River basin from spreading into the Great Lakes (Cuddington et al., 2014), where they could cause severe ecological and economic damage (Tsehaye et al., 2013). Management efforts to prevent spread to the Great Lakes can also reduce and possibly mitigate impacts occurring within the Illinois River (Sass et al., 2014), which provides an artificial hydrologic connection between the Mississippi River basin and the Great Lakes. The Invasive Carp Regional Coordinating Committee (ICRCC; previously Asian Carp Regional Coordinating Committee) consists of

international, federal, state, and municipal partners and organizes long-term management efforts (ICRCC, 2022). As one goal, the ICRCC seeks to minimize propagule pressure on a series of electric dispersal barriers located upriver from the current invasion front (Parker et al., 2016).

To achieve the goal of minimizing upriver propagule pressure and preventing range expansion, management actions have primarily focused on reducing abundance of adult bigheaded carps near the invasion front (Coulter, MacNamara, et al., 2018) and by taking advantage of existing movement deterrents (i.e. lock and dam structures) to limit upriver movement (Coulter, Brey, et al., 2018). Although removal efforts have been focused on reducing abundance near the invasion front (Coulter, MacNamara, et al., 2018), additional harvest farther downriver on the source population might also support the goal of minimizing propagule pressure upriver from the invasion front (Baker, 2017). Additionally, a variety of deterrence technologies have been investigated (Cupp et al., 2021) that, if effective, could be placed at existing navigation lock structures to further decrease passage. Assessing deterrent locations and effectiveness of harvest needed to elicit desired population responses will be important for successful long-term management as part of integrated approaches.

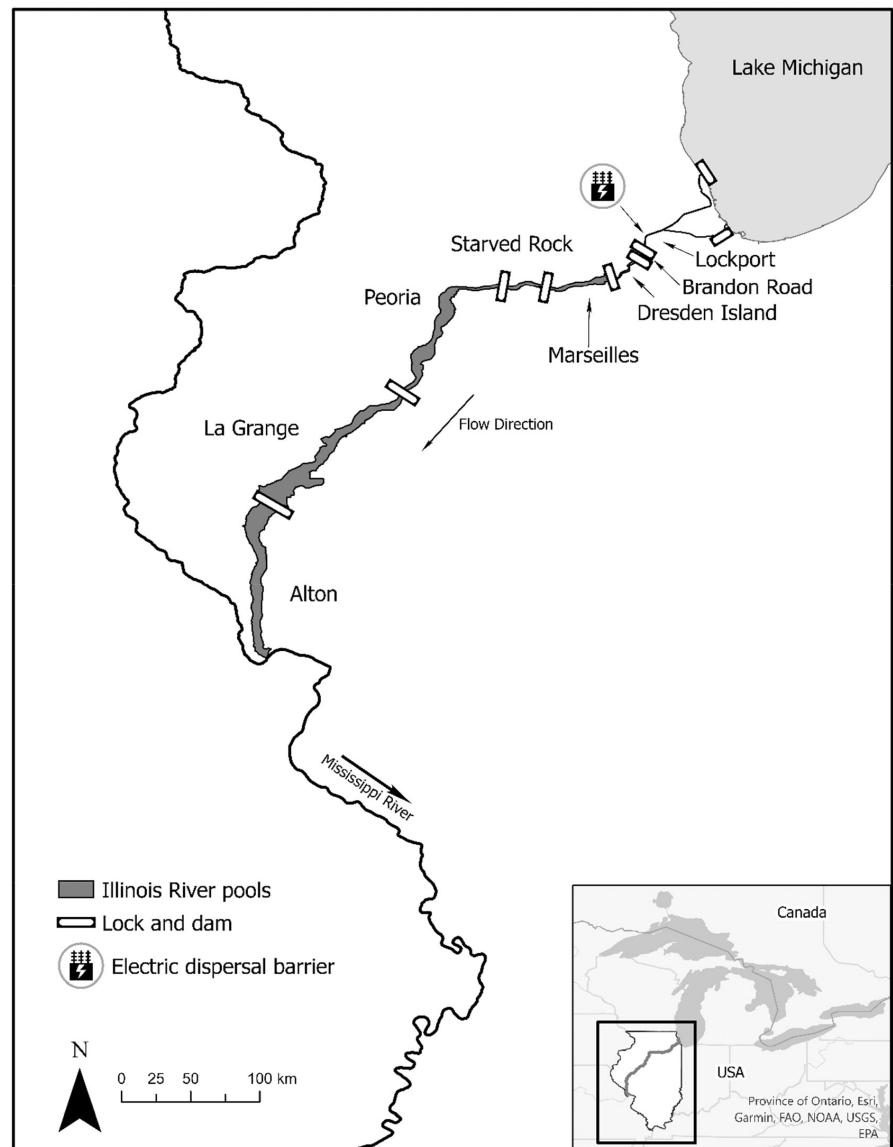
We developed a spatially explicit population model to assess the potential effects of alternative management actions on the invasive bigheaded carp populations of the Illinois River. A population model has previously been developed for bigheaded carp in this river (Tsehaye et al., 2013) however, the model did not account for metapopulation dynamics, which have been recently documented in bigheaded carp (e.g. spatial differences in growth, reproduction, and movement; Coulter, Brey, et al., 2018; Parkos et al., 2021). Therefore, the objectives of our study were to develop a spatially explicit population model for bigheaded carp in the Illinois River to assess the effects of the location and effectiveness of removal efforts and movement deterrents on population dynamics. This model, known as the spatially explicit invasive carp population (SEICarP) model, represents a conservation tool for predicting the effectiveness of directed management efforts to contain the spread of these invasive species and reduce population numbers.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The Illinois River, approximately 526 km long, connects the Mississippi River to Lake Michigan through the Chicago Sanitary and Ship Canal (Lian et al., 2012). The Illinois River includes a series of locks and dams, fragmenting the river into eight pools (Figure 1). Brandon Road and Lockport pools were excluded because they

**FIGURE 1** Pools of the Illinois River (Alton through Dresden Island pools) within which bigheaded carp population dynamics were modelled. Brandon and Lockport pools are included for reference.



are upriver of the current invasion front (i.e. Dresden Island Pool), which is 64 river km downriver of Lake Michigan. The remaining six pools (i.e. study area) can be grouped into lower river (Alton, La Grange, and Peoria pools; hereafter, lower river) and upper river pools (Starved Rock, Marseilles, and Dresden Island pools; hereafter, upper river) based on several characteristics. Pools in the lower river are longer (each ~130 river km) with flow conditions and connected backwater lakes allowing bigheaded carp reproduction and recruitment (Parkos et al., 2021; Sass et al., 2010) resulting in higher invasive carp densities relative to the upper river pools (Coulter, MacNamara, et al., 2018). Further, the wicket-style dams separating the pools in the lower river allow for relatively greater movement rates among pools during high flow (Coulter, Brey, et al., 2018). Limited commercial fishing for invasive carp occurs in the lower river. In contrast, upper river pools are relatively short (~23–40 river km) and lack connected backwaters. Adult densities are lower in the upper river (Coulter, MacNamara, et al., 2018) and recruitment does not appear to occur in these pools (McClelland

et al., 2012). Evidence suggests immigration from the lower river sustains bigheaded carp abundance in the upper river (Coulter, Brey, et al., 2018; McClelland et al., 2012; Sass et al., 2010). High-head dams with Tainter gates (see Koel & Sparks, 2002 for design descriptions) separate pools in the upper river, reducing movement rates and, thus, connectivity among upper river pools (Coulter, Brey, et al., 2018; Koel & Sparks, 2002). Intensive removal of bigheaded carp by state contracted commercial fishers occurs within the upper river to reduce adult abundances and, therefore, curb the risk of range expansion upriver toward Lake Michigan (MacNamara et al., 2016).

## 2.2 | Model structure

We developed a spatially explicit model simulating bigheaded carp population dynamics in annual time steps using survival, growth, inter-pool movement, and recruitment sub-models. [Table 1](#)

**TABLE 1** Input parameters for each species based upon sub-model. If parameters were constant across all pools, the parameter were not 'unique per pool'.

Sub-model	Parameter(s)	<i>n</i>	Unique per pool	Source
Movements	Between pool transitions	36	Yes	Coulter, MacNamara, et al. (2018) and Coulter, Brey, et al. (2018)
von Bertalanffy	Growth coefficient	1	No	Erickson, Kallis, Coulter, et al. (2021)
von Bertalanffy	Asymptotic maximum length	1	No	Erickson, Kallis, Coulter, et al. (2021)
von Bertalanffy	Natural mortality	1	No	Erickson, Kallis, Coulter, et al. (2021)
Female length-maturity	Intercept	1	No	Erickson, Kallis, Coulter, et al. (2021)
Female length-maturity	Slope	1	No	Erickson, Kallis, Coulter, et al. (2021)
Length-weight	Intercept	1	No	Erickson, Kallis, Coulter, et al. (2021)
Length-weight	Slope	1	No	Erickson, Kallis, Coulter, et al. (2021)
Ricker recruitment	Average recruitment without harvest per pool	6	Yes	Arbitrary, selected based upon pool length
Ricker recruitment	Unfished level of reproductive output per pool	6	Yes	Arbitrary, selected based upon pool length
Ricker recruitment	Steepness	1	No	Evaluated sensitivity analysis within this paper

summarizes all input parameters and their source. Sub-models were applied in sequential fashion, starting with survival. The number of fish (*N*) in pool *p* and length class *l* (class width=100mm, ranging from 100 to 1300mm) surviving to the next time step (next year) was calculated as

$$N_{p,l,t+1} = N_{p,l,t} (1 - M)(1 - v_l F_p),$$

where *M* is annual natural mortality rate (time, length and pool invariant) and *v<sub>l</sub>* and *F<sub>p</sub>* are user-defined terms representing length-specific harvest vulnerability and an additional harvest mortality rate, respectively. Mortality rates are finite rates for the fraction lost each year.

Following survival, annual growth of each length class is updated. Pool-specific populations, in terms of numbers in each length class, are multiplied by the probability of transitioning from the current length class to the next length class. Transition probabilities were calculated using an age-independent formulation of the von Bertalanffy growth function (Sullivan et al., 1990), which describes the change in length,  $\Delta l$ , over 1 year as a function of current length *l<sub>t</sub>*, asymptotic length *L<sub>∞</sub>*, and the growth coefficient *k*,

$$\Delta l = (L_{\infty} - l_t)(1 - e^{-k}).$$

Annual net movement among pools was then simulated by multiplying the number of individuals per pool by a movement probability matrix. Each element of the movement matrix describes the movement probability among the six pools included in the underlying movement model developed by Coulter, Brey, et al. (2018). Only fish larger than the length at 50% maturity were allowed to move between pools, reflecting observations by Coulter, Brey, et al. (2018) and long-term field results (e.g. dearth of sub-adult captures in upper river pools).

Recruitment is the final sub-model and was estimated using a Ricker stock-recruitment relationship (Ricker, 1954). The specific formulation of the Ricker model followed the formulation by Punt

and Methot (2005) which predicts the number of recruits (*R*) as a function of the average recruitment without harvest (*R<sub>0</sub>*), the spawning stock biomass (*B*), the unfished level of reproductive output (*S<sub>0</sub>*), and a steepness parameter (*h*),

$$R = R_0 \frac{B}{S_0} e^{(-\ln(5h)) \frac{B}{S_0} - 1} \frac{B - 1}{0.8}.$$

A von Bertalanffy growth function that predicts length as a function of the asymptotic maximum growth rate (*l<sub>∞</sub>*), growth coefficient (*k*), and age was used to calculate the length of age-1 fish

$$\text{length} = l_{\infty} (1 - e^{-k \times \text{age}}). \quad (1)$$

Specifically, age was set to 1 in Equation (1) to assign recruits to the length at age-1 length bin and then recruits were placed in the pool where spawning occurred.

### 2.3 | Model parameterization

We used data from fishery-independent and fishery-dependent collection efforts to estimate bigheaded carp demographic rates. A superset of data has been released as part of broader modelling efforts, which includes data from the Ohio and Mississippi rivers (Erickson, Kallis, Coulter, et al., 2021). The demographic rates used herein were based on data collected from pools in the Illinois and upper Mississippi rivers during 1997–2015 (see online Supporting Information for silver and bighead carp model inputs).

We used methods from Midway et al. (2015) to fit Bayesian hierarchical models, specifically a von Bertalanffy growth curve, a function that relates the probability of female maturity to their length, and a length-weight relation. Equations 1–3 in Midway et al. (2015) present the von Bertalanffy growth curve and Equations 5–7 in

Midway et al. (2015) present the logistic model used for the probability of female maturity as a function of length. The  $\log_{10}$ - $\log_{10}$  length-weight relation was modelled using a similar mode, but is not included in Midway et al. (2015) so the equations are included here, which include an intercept,  $\alpha_j$ , a slope  $\beta_j$ , and a hierarchical error term,  $\epsilon_{ij[j]}$  for each pool,  $j$ ,

$$\log_{10}(\text{length}) \sim \alpha_j + \beta_j \log_{10}(\text{weight}) + \epsilon_{ij[j]},$$

$$\ln \begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim \text{MVN}(\mu, \Sigma), \text{ and}$$

$$\mu \sim \ln(\bar{\alpha}, \bar{\beta}).$$

Although we were able to fit models for specific pools, our uncertainty estimates were unreasonable, so we used the hierarchical estimate across all pools for each pool. We used the approach of Then et al. (2015) to estimate natural mortality as a function of growth parameters and used movement data from Coulter, Brey, et al. (2018). Our movement data (Coulter et al., 2022) differed slightly from Coulter, Brey, et al. (2018) because we used movements drawn from MCMC chains generated in Program MARK from the top-performing models (Coulter, Brey, et al., 2018) rather than using the summary data presented in the original paper for both bighead and silver carp (Kallis et al., 2021).

A Ricker stock-recruitment model, expressed in terms of steepness of the relationship, characterized adult spawning to age-1 survival for each pool. Conditions conducive to strong recruitment such as suitable flow and temperature likely covary through time among pools (Sullivan et al., 2018). Thus, we assumed that if recruitment occurred in one pool, it occurred in all recruiting pools. The steepness parameterization requires three terms including recruitment ( $R_0$ ) and spawning stock biomass ( $S_0$ ) levels from an unfished population and steepness ( $h$ ), which is defined as the proportion of  $R_0$  at 20% of  $S_0$  (Kinzey et al., 2019). Values for the initial slope of the stock-recruitment relationship (Tsehaye et al., 2013) were converted to  $h$ , for each species. Appropriate  $S_0$  and  $R_0$  values were not available for our study species. Thus, we set  $R_0$  in the largest pool included in our study (i.e. Alton Pool) to an arbitrary value of 1000 and scaled the remaining values by pool length. The value of 1000 was selected because population estimates do not exist for the Illinois River, and managers use our model to understand where in the Illinois River, the relative amount, and what size fish to harvest rather than the absolute number to harvest. Ideally, population sizes in the model could be matched to empirical estimates, but those estimates do not exist at this time. Values of  $S_0$  for each pool were calculated as a function of  $R_0$  by assuming a stable length distribution using mean demographic rates.

## 2.4 | Initial populations

The model was initialized using stable length distributions constructed from mean demographic rates (i.e. the stable length

distributions based upon prior runs were used for the simulations initial conditions). Initial abundances were determined using the stock-recruitment functions for each pool. Specifically, we set the pool with highest density of bigheaded carp (silver carp: La Grange; bighead carp: Peoria) to  $S_0$  and scaled the remaining pools using hydroacoustics density estimates (Coulter, MacNamara, et al., 2018), thus preserving the relative differences in abundance among pools. Lastly, consistent with field data where small bigheaded carp are not observed in the upper pools and our assumption about size-dependent movement between pools, fish smaller than the length at 50% maturity were not included in initialized populations in the upper pools.

## 2.5 | Model uncertainty

The model incorporated two levels of uncertainty: variability in demographic and movement rates and temporal variance in recruitment. Uncertainty in demographic and movement rates was incorporated by repeating 25-year simulations for each management scenario using 100 iterations. Growth, maturity, natural mortality, length-weight and movement parameters were randomly selected from the Bayesian posterior distributions for each parameter and then used to predict expected inputs for the model. Interannual (temporal) variability in reproductive success (i.e. year class failure and success) was included using a Bernoulli distribution (Gibson-Reinemer et al., 2017). For each annual time step, the number of individuals estimated from the stock-recruitment functions was added to the populations with probability 0.5. This probability was estimated from the relative frequency of historically observed successful reproduction events in the La Grange pool of the Illinois River. The data used were for 2000 to 2015 from the USGS Long-Term Resource Monitoring (LTRM) element of the Upper Mississippi River Restoration Program data ([https://umesc.usgs.gov/data\\_library/fisheries/fish\\_page.html](https://umesc.usgs.gov/data_library/fisheries/fish_page.html), Accessed 5 July 2023). Annual data were used to classify reproduction in a pool as successful when the catch of age-0 fish (i.e. <250 mm total length [TL]) was >0.

## 2.6 | Simulated management scenarios

We evaluated bigheaded carp population responses to possible management actions of additional harvest mortality and decreased upriver movement rates, with each species modelled separately. We simulated different combinations of fractional harvest mortality (0–1 in 0.25 intervals) in the lower (Alton, LaGrange, Peoria) and upper river (Starved Rock, Marseilles, Dresden Island). Harvest mortality was limited to fish greater than 500 mm total length.

Effects of upriver movement deterrents on bigheaded carp populations were simulated under different combinations of deterrent efficiencies, including reductions of 0.25, 0.50, and 0.75 of baseline movement values at Starved Rock, Marseilles, and Dresden Island Lock and Dam. Thus, if bigheaded carp had a 10% probability



of moving between two pools, a reduction of 0.25 would have a movement probability of 7.5%. We conducted separate simulations evaluating effects of increased adult harvest mortality and upriver movement deterrence, as well as selected combinations of both being imposed together. Specifically, we examined all combinations of upper and lower harvest rates of 0 and 0.25 (4 scenarios), deterrent locations at each of the three upper locks (3 scenarios), and three deterrent levels (0.25, 0.5, and 0.75) for a total of 36 different scenarios.

Proportional change in bigheaded carp abundance relative to the no action, *reference*, scenario (i.e. zero harvest mortality and baseline movement rates) was used to quantify and compare performance of the possible management actions in the leading edge of the invasion (i.e. Dresden Island Pool). Proportional change was calculated at the end of each 25-year simulation by dividing the number of fish alive in Dresden Island Pool by the number alive under the reference scenario. We also included the relative changes for harvest scenarios for all pools in Supporting Information (Erickson, Kallis, & Glover, 2021). We performed 100 replicate simulations for each management scenario to capture the effects of demographic parameter and temporal variability in reproductive success. We used the same realization of stochastic replicates (demographic rates and stochastic spawning years) for all harvest and movement management scenarios to generate results that only differed by the specific management actions while including stochasticity. We compared possible management scenarios with respect to their ability to achieve a 90% reduction in proportional change values. This metric measures the likelihood that a specific set of management actions would result in a leading-edge pool abundance that was  $\leq 90\%$  than the reference simulation.

### 3 | RESULTS

Predicted abundances by pool under reference conditions showed quasi-stable equilibria in all pools with the upper pools requiring about a 5-year transition period (Figure 2). Populations generally persisted in each pool (except Marseilles for silver carp), with population abundances higher in the lower pools than the upper pools. Although rare, certain stochastic realizations went functionally extinct ( $<10$  individuals) in each pool. Extinctions were associated with extreme combinations of parameter values (e.g. extremely large size at maturity and low growth rates). The Marseilles population of silver carp became functionally extinct within the model with most stochastic realizations resulting in a population less than 10 individuals within 10 years (Figure 2).

Model simulations showed that harvest mortality as the solo management tool was more effective when applied to the lower river compared to when applied to the upper river (Figure 3). The model predicted a strong response in silver carp abundance at model year 25 with increasing harvest in the lower Illinois River. The model also predicted that bighead carp populations would immediately decrease in response to increased lower river harvest. Both species showed little response to increased upper river harvest for a given

level of lower river harvest. For example, the probabilities of reaching target reduction levels (i.e. 90% change) for silver carp at the invasion front (Dresden Island Pool) were 17%, 45%, 90% and 100% at lower river harvest mortality rates of 0.25, 0.5, 0.75, and 1.0, respectively. In contrast, the probability of achieving target reduction levels using an upper river only harvest strategy was relatively low (5%, 12%, 26% and 34% for the same respective levels of silver carp harvest). Indeed, setting upper river harvest mortality to a high level (i.e. 1.0) still required an additional lower river harvest mortality rate of 0.3–0.4 to have a 50% probability of reaching the target reduction level.

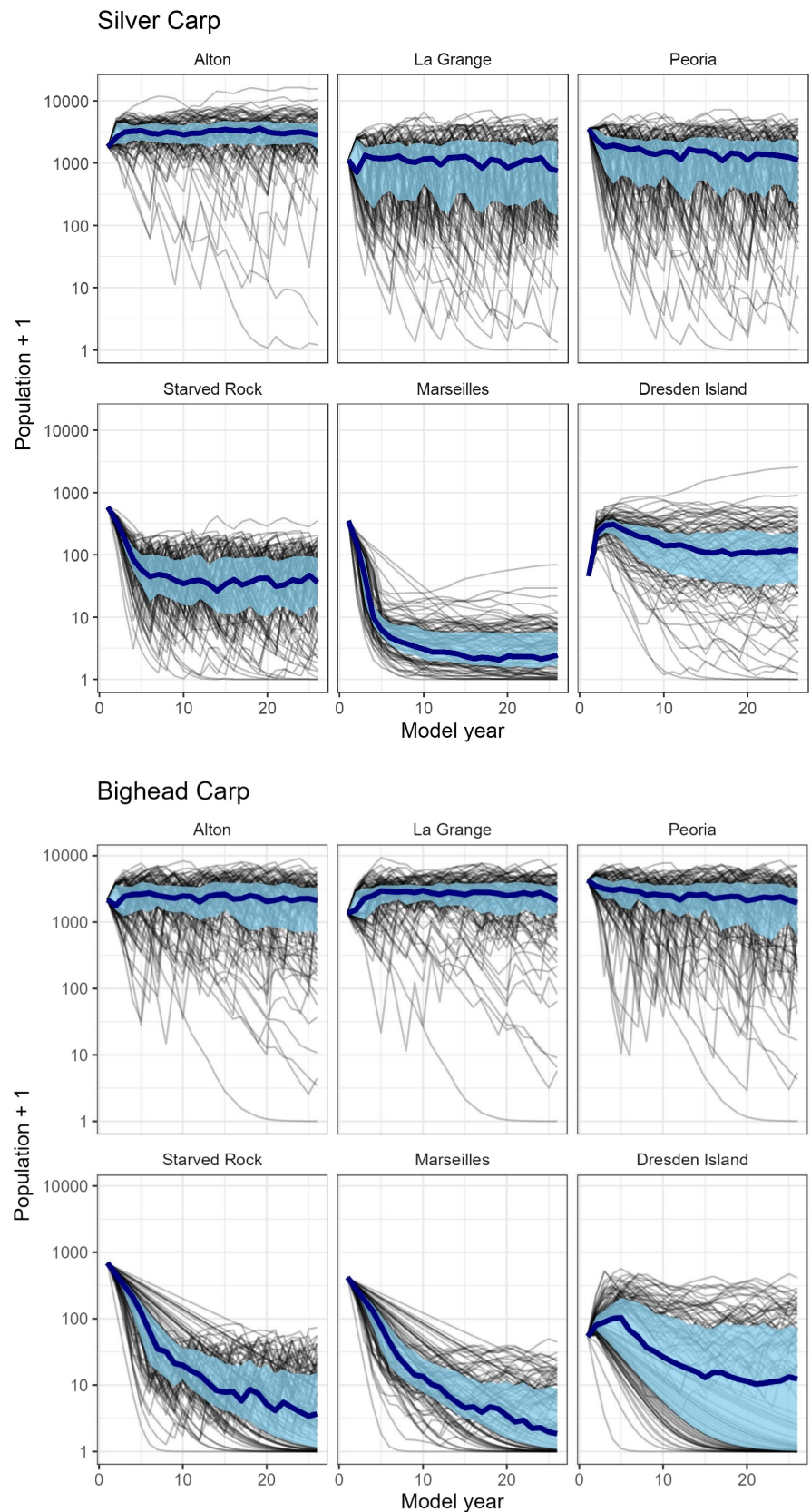
Model results also showed the influence of deterrents on Dresden Island Pool target levels. Movement deterrents strongly influenced the relative population of bigheaded carp in the Dresden Island Pool (Figure 4). Additionally, a pattern emerged for bigheaded carp when the deterrent was located farther downriver in the upper river. Specifically, the placement caused a greater decrease in the relative Dresden Island population size compared to placing the deterrent farther upriver (e.g. the model indicated that the placement of a deterrent system would be more effective for controlling upriver populations if it were placed at Starved Rock Lock and Dam compared to Dresden Island Lock and Dam).

This pattern emerged consistently across harvest mortality levels for both silver and bighead carp simulations. Although movement deterrents reduced Dresden Island population size, deterrent-only strategies could not achieve target reduction levels, even at high deterrence rates. For example, the probability of reaching the target reduction level for silver carp was only 1% for a deterrent with high effectiveness (i.e. 0.75) placed at the optimal location (i.e. Starved Rock Lock and Dam). Including an additional 0.25 harvest mortality in the upper and lower river pools, however, resulted in a 9% probability of reaching the target reduction level (Figures 3 and 4).

### 4 | DISCUSSION

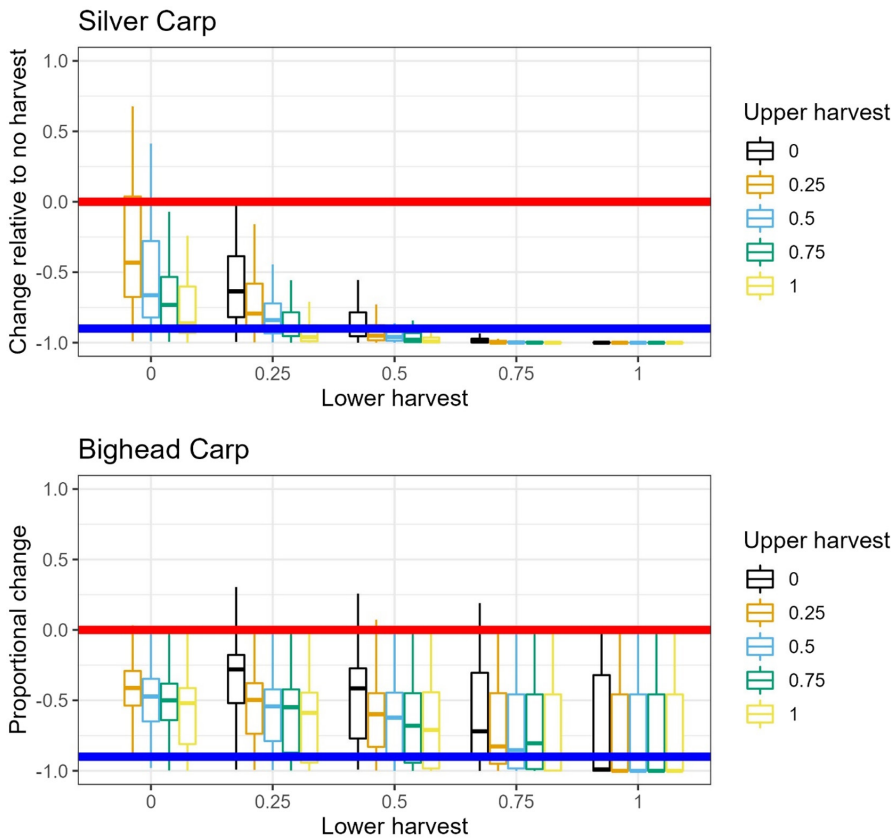
Our development and use of the SEICarP model highlight the importance of metapopulation dynamics when evaluating invasive species management options. Model results indicated that changes to historical management actions, particularly through the location of additional harvest, could have a greater effect on achieving long-term management goals than the historical management actions alone (Epanchin-Niell & Wilen, 2012). We also identified specific geographic locations where new movement deterrent technologies may be most effective at inhibiting upriver movement from source populations. Investigations into efficacies of deterrents in these locations may help further identify management alternatives and could be used in future model predictions. Accounting for such spatial dynamics when evaluating management options can result in improved control outcomes as well as strategies that are more cost effective (Lustig et al., 2019). These findings will allow for the most adaptive and proactive management planning when developing long-term strategies to combat these invasive species.

**FIGURE 2** Modelled bigheaded carp abundances under the reference scenario. Replicate simulations (100) are indicated by separate lines. The sky-blue ribbons are the middle 50% of data and the navy-blue line is the median population size. Note the  $\log_{10}(n+1)$  y-axis scale.



Incorporating spatial dynamics and size-dependent movement into our model indicated that the best additional actions to take to achieve long-term conservation goals are to adopt different

management strategies for the upper and lower Illinois River. Limiting invasion risk to the Great Lakes via reducing abundance at the invasion front (Dresden Island Pool) can be accomplished using a size



**FIGURE 3** Proportional change in the abundance of bigheaded carp in Dresden Island Pool (i.e. invasion front) of the Illinois River after 25-year simulations of varying harvest scenarios. Proportional change is relative to the reference scenario (i.e. zero harvest mortality, baseline movement rates). A harvest of 1 represents 100% of fish being removed annually and a harvest of 0 indicates no harvest. A proportional change of zero indicates that a scenario had the same effect as the no-harvest reference scenario (red line), and the blue line indicates a 90% decrease in the population size relative to the no-harvest reference scenario (target reduction levels). Outliers are not displayed.

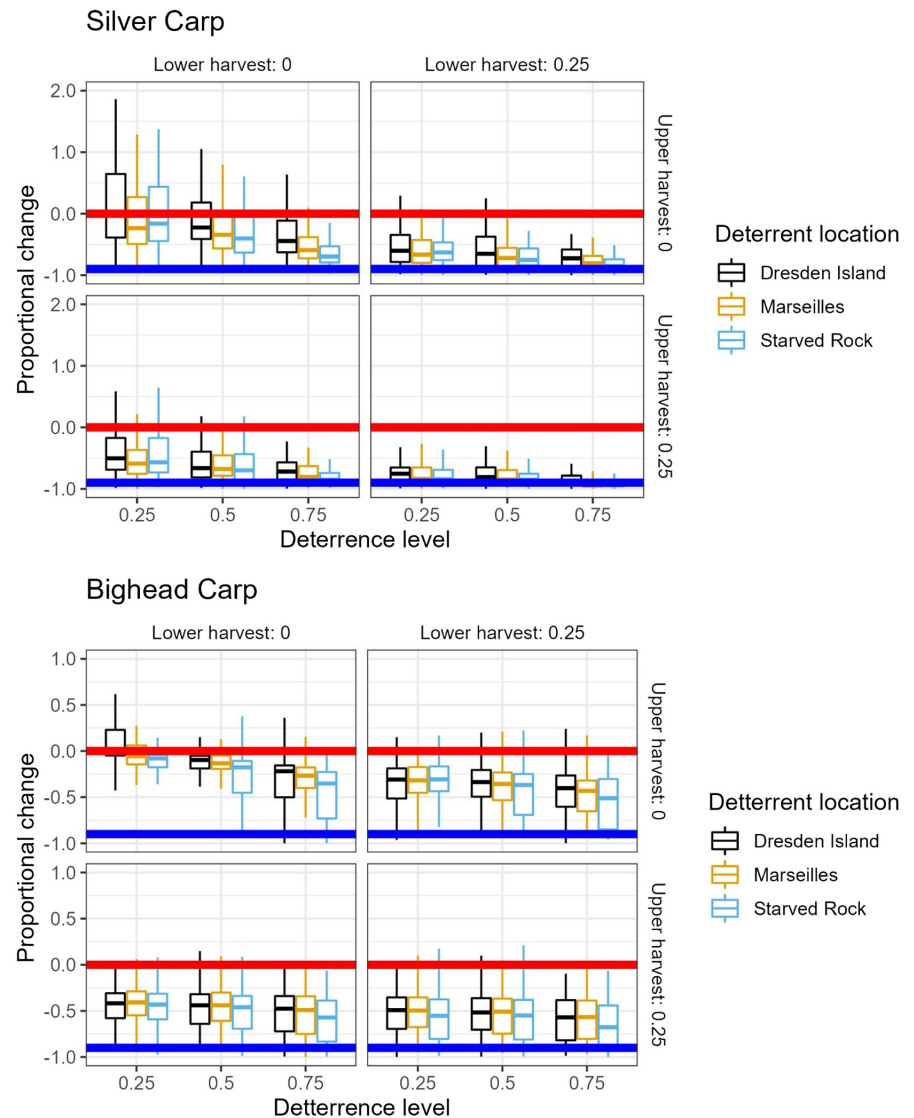
selective harvest strategy (e.g. harvesting fish longer than 500 mm) with relatively low exploitation rates targeting critical source locations. A previous modelling effort suggested harvest across all sizes may be needed to collapse the population (Tsehaye et al., 2013) but our model, which incorporates additional spatial details, reveals this is not necessary for reducing upper river abundance, specifically the population in Dresden Island.

Removals focused on large individuals can have multiplying benefits on native ecosystem recovery and management outcomes (Love et al., 2018; Tamburello et al., 2019). Upper river harvest strategies near the invasion front continue to be effective (Coulter, MacNamara, et al., 2018; MacNamara et al., 2016) because they directly reduce abundance and upriver dispersal at or near the invasion front. Our model results support the need for continuing upper river harvest as a control strategy, recognizing that additional harvest efforts allocated toward lower river pools can have markedly stronger effects on their own, and in tandem may be the optimal scenario for managers. The model identifies that harvest mortality rates, if achievable in the lower river environment, can be more effective at controlling the population at the invasion front than the same harvest mortality rate within upper river populations exclusively. This second emphasis on downriver harvest may be counter-intuitive. However, downriver populations are considerably larger than upriver populations and function as source populations within the model. Thus, the same percent reduction in a downriver pool has a greater effect than a similar reduction in an upriver pool.

The ability of achieving target mortality rates in the model, across varying and increasing heterogeneous habitats as one moves down the Illinois River with commercial, contracted, or other target fishing alone will depend on bioeconomics, but relationships among cost, mortality, and fish density are not well understood at this time. Disrupting metapopulation dynamics in this manner, and thereby inhibiting population connectivity among habitat patches, has also been a superior approach to containing and controlling other invasive species (Baker, 2017). Comparing the results for bighead versus silver carp, the model outputs were generally qualitatively similar, (i.e. harvesting the source populations rather than the sink populations and disconnecting the upper and lower river populations resulted in the strongest population declines). We did not have enough confidence in our model's input data to provide pool specific guidance, which might differ between species, especially for harvest.

The Marseilles Pool's functional extinction of silver carp reflects multiple components of the model. First, we scaled the model to have 10,000's of fish in the highest population pool, but best estimates from over a decade ago are at least an order of magnitude larger than this (Sass et al., 2010) and likely at least two orders of magnitude greater based upon ongoing harvest levels. Second, this extinction observation is likely a modelling artefact of the current movement data (e.g. Coulter, Brey, et al., 2018) that favours a stable distribution with most individuals in the ends of the river (i.e. Alton, Dresden Island pools). Empirically updated and more representative of actual population movement data would likely change this model

**FIGURE 4** Proportional change in the abundance of bigheaded carp in Dresden Island Pool (i.e., invasion front) of the Illinois River after 25-year simulations of varying harvest levels and location and efficacy of upriver movement deterrents. Proportional change is relative to the reference scenario (i.e. zero harvest mortality, baseline movement rates). The efficacy of upriver movement deterrents reflected a proportional decrease in upriver movement rates under reference scenarios. A harvest of 0.25 reflects 25% of fish being removed annually from either all upper or lower pools, and harvest of 0 corresponds to no harvest. A proportional change of zero indicates that a scenario had the same effect as the no-harvest reference scenario (red line), and the blue line indicates a 90% decrease in the population size relative to the no-harvest reference scenario (target reduction levels). Outliers are not displayed. Note the different y-axis scales.



artefact. Ultimately, for our applications of the SEICarP model, the absolute population is not important and avoiding realistic population sizes assists users of the model to realize the paucity of empirical population estimates for bigheaded carps in the Illinois River. Third, if the relatively small Marseilles population size is not a modelling artefact, then the pool is still important as a movement corridor even if it only has a small population and highlights the importance of movement deterrents.

Similar to harvest scenarios, model simulations involving the deterrence of upriver movement rates produced considerable reductions in abundance at the invasion front (Dresden Island Pool) by inhibiting connectivity between the lower river source populations with the upper river sink populations. Reducing connectivity among patches with existing deterrents, such as lock and dam structures, increases the effectiveness of harvest (Lustig et al., 2019) and could destabilize metapopulations (Lurgi et al., 2016). Variability in connectivity is also likely important as flow conditions change (Zielinski & Sorensen, 2021) but was not included due to a paucity of empirical data. These effects are evident in model outcomes, even with

the lack of any fish specific deterrent at locks and dams do limit fish movement at various rates based upon construction design and operating parameters and goals.

Behavioural deterrents (e.g. acoustics, light, carbon dioxide; Cupp et al., 2021) could be a way to add additional effectiveness to these existing lock and dam structures while maintaining normal operations. These approaches have varying levels of effectiveness (Noatch & Suski, 2012), and while our model only explores the location and effectiveness of generic movement deterrent parameters, estimates based upon deterrent evaluations could be inserted to provide more specific evaluations at various locations for efficacy predictions for management consideration. The strongest effects of an enhanced movement deterrent were realized at Starved Rock Lock and Dam, intermediate at Marseilles, and weakest at Dresden Island, similar to results from Coulter, Brey, et al. (2018). This result reflects the benefit of containing source populations to downriver pools that support bigheaded carp reproduction and recruitment. Although our results suggest that Starved Rock Lock and Dam would be the most effective deterrent location, this recommendation is



based solely on impacts to bigheaded carp. Actual implementation must consider efficacy across variable hydrological regimes and seasons, impacts to native aquatic species (Altenritter et al., 2019), overall reliability, economic costs, and other considerations, all of which would likely vary with deterrent location. For example, ongoing efforts such as the Brandon Road Interbasin Project by the U.S. Army Corps of Engineers (<https://www.mvr.usace.army.mil/Missions/Environmental-Stewardship/BR-Interbasin-Project/>, accessed 5 July 2023) is currently considering multiple different structural and non-structural control measures such as those we previously list.

Our results also highlight the compounding benefits associated with using an integrated pest management strategy for invasive species control. The combination of additional lower river harvest and enhanced movement deterrents to inhibit connectivity among habitat patches (i.e. river pools) in our study provided relatively high reductions in bigheaded carp abundance at the invasion front. Using multiple management approaches would diversify risk if additional uncertainties not accounted for in the model are realized (e.g. juvenile fish moving between pools; juvenile fish produced in upper river pools) and if one or more control options becomes temporarily ineffective, such as during a maintenance or outage event of a movement deterrent technology or flooding and freezing that prevent harvest or movement deterrent technologies. Multiple control strategies can also complement one another where the strengths of one approach (e.g. deterring movements of all sized individuals) can account for limitations of another (e.g. harvest targeting only larger individuals). Similar to other assessments of invasive species control programs (Brown & Gilligan, 2014; Walker et al., 2015), integrating multiple control efforts, when possible, would help optimize control approaches.

While our model predictions can inform future decisions on where and how to manage bigheaded carp, the diverse sources of data (e.g. growth, movement, recruitment, survival) needed by such modelling efforts required us to make simplifying assumptions that could affect the accuracy of our predictions; such limits are inherent in all biological models but can be reduced with review and update as well as additional data. One identified need is for increased spatial and temporal resolution of movement rates among pools. The model currently assumes constant, monthly movement rates (Coulter, Brey, et al., 2018), although additional movement data could identify monthly or seasonally variable movement rates among pools that could enhance model predictions and improve management effectiveness by reducing uncertainty (Pepin et al., 2020). Additional uncertainties include specific density dependent mechanisms that can affect exploited fish populations (Rose et al., 2001); in our case, how to represent density-dependent movement rates among pools. Finally, stock-recruitment models form the basis of many fisheries models (Shepherd & Cushing, 1980), yet we do not have a sufficient understanding of this relationship for bighead and silver carp in the Illinois River to incorporate into the model. Work by Hoff et al. (2011) has provided quantitative insight into bigheaded carp recruitment in the Illinois River, but their units mis-matched with ours because they did not account for differences in catchability of adults and recruits.

Although sensitivity analysis indicated that our results (i.e. proportional declines in abundance) were largely insensitive to the steepness parameter in this relationship (Erickson, Kallis, & Glover, 2021), future work is required to better understand the sensitivity of model predictions to other input parameters such as the size of fish moving in the model.

Identifying these data limitations now provides opportunities for directing future research, as we can use model limitations and information gaps to inform future data collection and analyses. For example, understanding seasonal movement patterns of bigheaded carp could inform the timing of harvest events, whereas understanding density-dependent movement responses could help refine mortality targets needed to reduce upriver dispersal or provide insights into the consequences of concentrating fish below potential movement deterrent barriers. While our model has opportunities for enhancing areas of data limitation, invasive species management for achieving conservation goals is time sensitive. Therefore, our model predictions provide the best to-date quantitative assessment of alternative management actions that resource managers can use for making informed, long-term conservation decisions. Overall, our results support previous work suggesting that metapopulations can be managed by suppressing source populations (Baker, 2017; Perry et al., 2017), reducing dispersal (Lurgi et al., 2016), and combining multiple strategies can lead to more effective control (Davis et al., 2021; Day et al., 2018). In the long term, using metapopulation modelling to inform conservation strategies will increase effectiveness of management programs (Lustig et al., 2019).

Our general modelling approach can be used to develop metapopulation models for other species invasions, including invasions that have limited demographic or spatially-explicit data. Initial model parameterization could be performed with data from their native range or information from similar species. Initial response actions should be treated as opportunities for data collection to update the model as new data become available. The model should then be assessed to understand how assumptions and uncertainties influence model predictions, and the results used to prioritize additional data collection needs. Data collection should be coordinated among multiple stakeholder groups to rapidly obtain data over a broad spatial scale and to reduce effort and costs for individual stakeholder groups. Finally, modellers must work closely with resource managers when identifying future data needs and developing model objectives. This will allow model simulations to be of direct use to managers based on their logistical limitations and available management tools. Without early and consistent engagement from resource managers, any modelling results will likely not be used to inform decision making.

#### AUTHOR CONTRIBUTIONS

Jahn Kallis, David Coulter, Alison Coulter, James Garvey, Marybeth Brey, Matt Catalano, John Dettmers, Kevin Irons, Elizabeth Marschall, Kenneth Rose, Mark Wildhaber and David Glover conceived the ideas and methodology; Jahn Kallis, David Glover, and Richard Erickson compiled and analysed the data; Jahn Kallis,

Richard Erickson, David Coulter and David Glover led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

Data available from Open PRAIRIE repository [https://openprairie.sdstate.edu/nrm\\_datasets/3](https://openprairie.sdstate.edu/nrm_datasets/3) (Coulter et al., 2022) and U.S. Geological Survey software release <https://doi.org/10.5066/P9DPL997> (Kallis et al., 2021).

## ORCID

Jahn Kallis  <https://orcid.org/0000-0002-7930-6656>  
 Richard Erickson  <https://orcid.org/0000-0003-4649-482X>  
 David Coulter  <https://orcid.org/0000-0001-8414-2505>  
 Alison Coulter  <https://orcid.org/0000-0002-5604-6513>  
 Marybeth Brey  <https://orcid.org/0000-0003-4403-9655>  
 John Dettmers  <https://orcid.org/0000-0003-1061-210X>  
 James Garvey  <https://orcid.org/0000-0001-5393-9351>  
 Elizabeth Marshall  <https://orcid.org/0000-0002-8026-4203>  
 Kenneth Rose  <https://orcid.org/0000-0002-9310-8410>  
 Mark Wildhaber  <https://orcid.org/0000-0002-6538-9083>  
 David Glover  <https://orcid.org/0000-0001-6532-1815>

## REFERENCES

- Altenritter, M. E., Pescitelli, S. M., Whitten, A. L., & Casper, A. F. (2019). Implications of an invasive fish barrier for the long-term recovery of native fish assemblages in a previously degraded northeastern Illinois River system. *River Research and Applications*, 35(7), 1044–1052.
- Baker, C. M. (2017). Target the source: Optimal spatiotemporal resource allocation for invasive species control: Optimal invasive species control. *Conservation Letters*, 10(1), 41–48. <https://doi.org/10.1111/conl.12236>
- Brown, P., & Gilligan, D. (2014). Optimising an integrated pest-management strategy for a spatially structured population of common carp (*Cyprinus carpio*) using meta-population modelling. *Marine and Freshwater Research*, 65(6), 538. <https://doi.org/10.1071/MF13117>
- Chapman, D. C., Benson, A. J., Embke, H. S., King, N. R., Kočovský, P. M., Lewis, T. D., & Mandrak, N. E. (2021). Status of the major aquaculture carps of China in the Laurentian Great Lakes Basin. *Journal of Great Lakes Research*, 47(1), 3–13. <https://doi.org/10.1016/j.jglr.2020.07.018>
- Coulter, A. A., Brey, M. K., Lubejko, M., Kallis, J. L., Coulter, D. P., Glover, D. C., Whitley, G. W., & Garvey, J. E. (2018). Multistate models of bigheaded carps in the Illinois River reveal spatial dynamics of invasive species. *Biological Invasions*, 20(11), 3255–3270. <https://doi.org/10.1007/s10530-018-1772-6>
- Coulter, A. A., Brey, M. K., Lubejko, M. V., Kallis, J. L., Coulter, D. P., Whiteledge, G. W., & Garvey, J. E. (2022). Movement probabilities of bigheaded carps (*Hypophthalmichthys* spp.) in the Illinois River estimated from Markov chain Monte Carlo methods. Report No. 3. [https://openprairie.sdstate.edu/nrm\\_datasets/3](https://openprairie.sdstate.edu/nrm_datasets/3)
- Coulter, D. P., MacNamara, R., Glover, D. C., & Garvey, J. E. (2018). Possible unintended effects of management at an invasion front: Reduced prevalence corresponds with high condition of invasive bigheaded carps. *Biological Conservation*, 221, 118–126. <https://doi.org/10.1016/j.biocon.2018.02.020>
- Cuddington, K., Currie, W. J. S., & Koops, M. A. (2014). Could an Asian carp population establish in the Great Lakes from a small introduction? *Biological Invasions*, 16(4), 903–917. <https://doi.org/10.1007/s10530-013-0547-3>
- Cupp, A. R., Brey, M. K., Calfee, R. D., Chapman, D. C., Erickson, R., Fischer, J., Fritts, A. K., George, A. E., Jackson, P. R., Knights, B. C., Saari, G. N., & Kočovský, P. M. (2021). Emerging control strategies for integrated pest management of invasive carps. *Journal of Vertebrate Biology*, 70(4). <https://doi.org/10.25225/jvb.21057>
- Davis, A. J., Farrar, R., Jump, B., Hall, P., Guerrant, T., & Pepin, K. M. (2021). An efficient method of evaluating multiple concurrent management actions on invasive populations. *Ecology*, 32, e2623. <https://doi.org/10.1002/eap.2623>
- Day, C. C., Landguth, E. L., Bearlin, A., Holden, Z. A., & Whiteley, A. R. (2018). Using simulation modeling to inform management of invasive species: A case study of eastern brook trout suppression and eradication. *Biological Conservation*, 221, 10–22. <https://doi.org/10.1016/j.biocon.2018.01.017>
- Epanchin-Niell, R. S., & Wilen, J. E. (2012). Optimal spatial control of biological invasions. *Journal of Environmental Economics and Management*, 63(2), 260–270. <https://doi.org/10.1016/j.jeem.2011.10.003>
- Erickson, R., Kallis, J. L., Coulter, A. A., Coulter, D. P., MacNamara, R., Lamer, J. T., Bouska, W. W., Irons, K. S., Solomon, L. E., Stump, A. J., Weber, M. J., Brey, M., Sullivan, C. J., Sass, G. G., Garvey, J. E., & Glover, D. C. (2021). Demographic rate variability of bighead and silver carps along an invasion gradient. *Journal of Fish and Wildlife Management*, 12(2), 338–353. <https://doi.org/10.3996/JFWM-20-070>
- Erickson, R. A., Kallis, J. L., & Glover, D. C. (2021). Application of the SEICarP model to the Illinois River: U.S. Geological Survey software release. <https://doi.org/10.5066/P9M6SJ7J>
- Gibson-Reinemer, D. K., Solomon, L. E., Pendleton, R. M., Chick, J. H., & Casper, A. F. (2017). Hydrology controls recruitment of two invasive cyprinids: Bigheaded carp reproduction in a navigable large river. *PeerJ*, 5, e3641. <https://doi.org/10.7717/peerj.3641>
- Hoff, M. H., Pegg, M. A., & Irons, K. S. (2011). Management implications from a stock-recruit model for bighead carp in portions of the Illinois and Mississippi Rivers. In D. C. Chapman & M. H. Hoff (Eds.), *Invasive Asian carps in North America* (Vol. 74, pp. 5–14). American Fisheries Society.
- Invasive Carp Regional Coordinating Committee. (2022). 2022 invasive carp action plan. <http://invasivecarp.us/Documents/2022-Invasive-Carp-Action-Plan.pdf>

- Kallis, J. L., Erickson, R., Hebert, J. L., & Glover, D. C. (2021). *Spatially Explicit Invasive Carp (SEICarP) population model*. U.S. Geological Survey software release. <https://doi.org/10.5066/P9DPL997>
- Kinzey, D., Watters, G. M., & Reiss, C. S. (2019). Estimating recruitment variability and productivity in Antarctic krill. *Fisheries Research*, 217, 98–107.
- Koel, T. M., & Sparks, R. E. (2002). Historical patterns of river stage and fish communities as criteria for operations of dams on the Illinois river. *River Research and Applications*, 18(1), 3–19. <https://doi.org/10.1002/rra.630>
- Lian, Y., You, J.-Y., Sparks, R., & Demissie, M. (2012). Impact of human activities to hydrologic alterations on the Illinois River. *Journal of Hydrologic Engineering*, 17(4), 537–546.
- Love, S. A., Lederman, N. J., Anderson, R. L., DeBoer, J. A., & Casper, A. F. (2018). Does aquatic invasive species removal benefit native fish? The response of gizzard shad (*Dorosoma cepedianum*) to commercial harvest of bighead carp (*Hypophthalmichthys nobilis*) and silver carp (*H. molitrix*). *Hydrobiologia*, 817(1), 403–412. <https://doi.org/10.1007/s10750-017-3439-1>
- Lurgi, M., Wells, K., Kennedy, M., Campbell, S., & Fordham, D. A. (2016). A landscape approach to invasive species management. *PLoS ONE*, 11(7), e0160417. <https://doi.org/10.1371/journal.pone.0160417>
- Lustig, A., James, A., Anderson, D., & Plank, M. (2019). Pest control at a regional scale: Identifying key criteria using a spatially explicit, agent-based model. *Journal of Applied Ecology*, 56(7), 1515–1527. <https://doi.org/10.1111/1365-2664.13387>
- MacNamara, R., Glover, D., Garvey, J., Bouska, W., & Irons, K. (2016). Bigheaded carps (*Hypophthalmichthys* spp.) at the edge of their invaded range: Using hydroacoustics to assess population parameters and the efficacy of harvest as a control strategy in a large north American river. *Biological Invasions*, 18(11), 3293–3307. <https://doi.org/10.1007/s10530-016-1220-4>
- McClelland, M. A., Sass, G. G., Cook, T. R., Irons, K. S., Michaels, N. N., O'Hara, T. M., & Smith, C. S. (2012). The long-term Illinois River fish population monitoring program. *Fisheries*, 37(8), 340–350. <https://doi.org/10.1080/03632415.2012.704815>
- Midway, S. R., Wagner, T., Tracy, B. H., Hogue, G. M., & Starnes, W. C. (2015). Evaluating changes in stream fish species richness over a 50-year time-period within a landscape context. *Environmental Biology of Fishes*, 98(5), 1295–1309. <https://doi.org/10.1007/s10641-014-0359-z>
- Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6(9), 485–492. <https://doi.org/10.1890/070064>
- Noatch, M. R., & Suski, C. D. (2012). Non-physical barriers to deter fish movements. *Environmental Reviews*, 20(1), 71–82. <https://doi.org/10.1139/a2012-001>
- Paquet, M., Arlt, D., Knape, J., Low, M., Forslund, P., & Pärt, T. (2020). Why we should care about movements: Using spatially explicit integrated population models to assess habitat source–sink dynamics. *The Journal of Animal Ecology*, 89(12), 2922–2933. <https://doi.org/10.1111/1365-2656.13357>
- Parker, A. D., Glover, D. C., Finney, S. T., Rogers, P. B., Stewart, J. G., & Simmonds, R. L. (2016). Fish distribution, abundance, and behavioral interactions within a large electric dispersal barrier designed to prevent Asian carp movement. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(7), 1060–1071. <https://doi.org/10.1139/cjfas-2015-0309>
- Parkos, J. J., Butler, S. E., King, G. D., Porreca, A. P., Coulter, D. P., MacNamara, R., & Wahl, D. H. (2021). Spatiotemporal variation in the magnitude of reproduction by invasive, pelagically spawning carps in the Illinois waterway. *North American Journal of Fisheries Management*, 43, 112–125. <https://doi.org/10.1002/nafm.10634>
- Pepin, K. M., Smyser, T. J., Davis, A. J., Miller, R. S., McKee, S., VerCauteren, K. C., Kendall, W., & Sloatmaker, C. (2020). Optimal spatial prioritization of control resources for elimination of invasive species under demographic uncertainty. *Ecological Applications*, 30(6), e02126. <https://doi.org/10.1002/eap.2126>
- Perry, G. L. W., Moloney, K. A., & Etherington, T. R. (2017). Using network connectivity to prioritize sites for the control of invasive species. *Journal of Applied Ecology*, 54(4), 1238–1250. <https://doi.org/10.1111/1365-2664.12827>
- Punt, A. E., & Methot, R. D. (2005). The impact of recruitment projection methods on forecasts of rebuilding rates for overfished marine resources. In G. H. Kruse, V. F. Gallucci, D. E. Hay, R. I. Perry, R. M. Peterman, T. C. Shirley, P. D. Spencer, B. Wilson, & D. Woodby (Eds.), *Fisheries assessment and management in data-limited situations* (pp. 571–594). Alaska Sea Grant, University of Alaska Fairbanks.
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5), 559–623. <https://doi.org/10.1139/f54-039>
- Rose, K. A., Cowan, J. H., Winemiller, K. O., Myers, R. A., & Hilborn, R. (2001). Compensatory density dependence in fish populations: Importance, controversy, understanding and prognosis: Compensation in fish populations. *Fish and Fisheries*, 2(4), 293–327. <https://doi.org/10.1046/j.1467-2960.2001.00056.x>
- Sass, G. G., Cook, T. R., Irons, K. S., McClelland, M. A., Michaels, N. N., O'Hara, T. M., & Stroub, M. R. (2010). A mark-recapture population estimate for invasive silver carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. *Biological Invasions*, 12(3), 433–436.
- Sass, G. G., Hinz, C., Erickson, A. C., McClelland, N. N., McClelland, M. A., & Epifanio, J. M. (2014). Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research*, 40(4), 911–921. <https://doi.org/10.1016/j.jglr.2014.08.010>
- Shepherd, J. G., & Cushing, D. H. (1980). A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *ICES Journal of Marine Science*, 39(2), 160–167. <https://doi.org/10.1093/icesjms/39.2.160>
- Sullivan, C. J., Weber, M. J., Pierce, C. L., Wahl, D. H., Phelps, Q. E., Camacho, C. A., & Colombo, R. E. (2018). Factors regulating year-class strength of silver carp throughout the Mississippi River basin. *Transactions of the American Fisheries Society*, 147(3), 541–553. <https://doi.org/10.1002/tafs.10054>
- Sullivan, P. J., Lai, H.-L., & Gallucci, V. F. (1990). A catch-at-length analysis that incorporates a stochastic model of growth. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(1), 184–198. <https://doi.org/10.1139/f90-021>
- Tamburello, N., Ma, B. O., & Côté, I. M. (2019). From individual movement behavior to landscape-scale invasion dynamics and management: A case study of lionfish metapopulations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1781), 20180057. <https://doi.org/10.1098/rstb.2018.0057>
- Then, A. Y., Hoenig, J. M., Hall, N. G., & Hewitt, D. A. (2015). Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science*, 72(1), 82–92. <https://doi.org/10.1093/icesjms/fsu136>
- Tsehaye, I., Catalano, M., Sass, G., Glover, D., & Roth, B. (2013). Prospects for fishery-induced collapse of invasive Asian carp in the Illinois River. *Fisheries*, 38(10), 445–454. <https://doi.org/10.1080/03632415.2013.836501>
- Walker, A. N., Poos, J.-J., & Groeneveld, R. A. (2015). Invasive species control in a one-dimensional metapopulation network. *Ecological Modelling*, 316, 176–184. <https://doi.org/10.1016/j.ecolmodel.2015.08.015>
- Zielinski, D. P., & Sorensen, P. W. (2021). Numeric simulation demonstrates that the upstream movement of invasive bigheaded carp

can be blocked at sets of Mississippi River locks-and-dams using a combination of optimized spillway gate operations, lock deterrents, and carp removal. *Fishes*, 6(2), 10. <https://doi.org/10.3390/fishes6020010>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1:** Bighead carp inputs and silver carp inputs.

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